

SCUTACARUS BACULITARSUS MAHUNKA (ACARINA : SCUTACARIDAE)
PHORETIC ON THE MUSHROOM PHORID FLY
MEGASELIA HALTERATA (WOOD)

BY

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SUMMARY

Scutacarus baculitarsus (Acarina : Scutacaridae) was found clustered on the anterior abdomen of the phorid *Megaselia halterata* (Diptera : Phoridae) of both sexes. Mites were more aggregated on flies from the surroundings of a mushroom farm than from the beds where many flies were hibernating and carried a greater number of mites. Large numbers of mites were taken from the " casing layer " of one house by Tullgren extraction and the compost contained a " weed " mould. Detached mites reattached to both phorid and sciarid flies and " perched " in exposed positions from which they " ambushed " the host. Perching mites were studied with reference to the substrate, light, gravity and humidity and the mechanics of perching.

Mites were mass cultured using unsterilised brewer's yeast on a damp plaster substrate. Females became physogastric and laid near the colony while males carried away the quiescent chrysalis containing the phoretomorph females. The precociously developing male appeared to relate to a more exaggerated condition of parasitic males in *Acarophenax* and *Pyemotes*.

The association of the mite and its phorid host is discussed and considered to be assured only by particular ecological circumstance.

RÉSUMÉ

Scutacarus baculitarsus (Acarina : Scutacaridae) a été observé en groupes sur l'abdomen antérieur du phoride *Megaselia halterata* (Diptera : Phoridae) des deux sexes. L'agrégation des acariens sur des mouches provenant des environs d'une champignonnière était plus prononcée que chez celles qui provenaient de couches dans lesquelles hivernaient de grandes quantités de mouches qui portaient un plus grand nombre d'acariens. On a enlevé des acariens en grand nombre de la couche d'une seule chambre par la méthode d'extraction de Tullgren et on a trouvé dans le compost un champignon sauvage. Les acariens détachés se sont rattachés aux mouches phorides et aux mouches sciarides et on a remarqué qu'ils se perchent aux endroits exposés d'où ils guettent l'hôte. On a étudié les acariens par rapport au substrat, à la lumière, à la gravité, à l'humidité et au mécanisme des pattes (IV).

Les acariens ont été cultivés en masse à l'aide de la levure de bière non stérilisée sur un substrat de plâtre de moulage humide. Les femelles sont devenues physogastres et ont pondu leurs œufs près de la colonie tandis que les mâles ont emporté les chrysalides inactives contenant les femelles phorétomorphes.

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Acarologia, t. XXI, fasc. 1, 1979.

Il semble que le mâle précoce a rapport à une condition plus exagérée des mâles parasitiques chez *Acarophenax* et *Pyemotes*.

On discute de la relation entre l'acararien et son hôte phoride et on en conclut que celle-ci n'est assurée que par des circonstances écologiques particulières.

INTRODUCTION

Female scutacarid mites (males being undiscovered) are usually collected as new species in phoretic association with insects, particularly beetles (KARAFIAT, 1959) and Hymenoptera (DELFINADO & BAKER, 1976). For example, of 42 scutacarid species from an area studied by STAMMER (1952), 22 were phoretic. Little is known of their biology. Only in the species which is the subject of this paper (NORTON & IDE, 1974), in *S. acarorum* (KARAFIAT, 1959), in *S. tragariae* (RACK, 1975) and in the soil mite *S. agypticus*, which is saprophytic on the ant *Cataglyphus bicolor* Fab. (ELBADRY, YOUSEF & METWALLY, 1976), have the life-histories and immature stages been studied. Similarly the habitats of free-living scutacarids are barely defined (KARAFIAT, 1959). A considerable literature exists on techniques for their extraction from soil and litter (MURPHY, 1962) in which other species (e.g. KARAFIAT, 1959) are known to occur. Thus the Chilean type-location of *Scutacarus baculitarsus* Mahunka (Acarina : Scutacaridae) was given as wet litter from the outer side of bushes at a moist brook-side (MAHUNKA, 1968).

NORTON & IDE (1974) found small numbers of females of the subspecies *agaricus* of *S. baculitarsus* both in mushroom compost and on the host ; a phorid fly, *Megaselia dakotensis* Borgmeier (= *halterata* (Wood) ROBINSON, 1975) (Diptera : Phoridae)). HUSSEY (1959) claimed, from catches from light traps, that mushroom phorids carry mites much less frequently than do mushroom sciarid flies (Diptera : Sciaridae) (BINNS, 1972 ; 1973). This paper marks the first record of a *Scutacarus* associating with a dipterous insect as this genus, usually associates with beetles (KARAFIAT, 1959). Further observations of scutacarids occurring on both a phorid and a sphaerocerid (Diptera : Sphaeroceridae) have since been confirmed in New Zealand (MARTIN, N. ; D.S.I.R. Auckland ; personal communication).

From 400 flies sampled NORTON & IDE (1974) recorded only 2 % infestation at two sites with a maximum of four mites per fly. A much higher level of infestation was discovered in October 1976 at a mushroom farm at Oving, nr. Chichester, Sussex. Mites occurred in such numbers as to facilitate studies on many aspects of scutacarid biology.

MATERIALS AND METHODS

The farm at which the discovery was made had a long-standing history of infestation of the phorid *Megaselia halterata* as well as some problems with the "weed mould" *Trichothecium roseum* Link. (Eumycota : Hyphomycetes) in the compost.

Large numbers of phorids could be seen both inside and around the mushroom houses (HUSSEY, 1959) and the opportunity was therefore taken to sample not only phorid fly populations from different points around the farm but also the mushroom beds themselves and to examine the behaviour of the phoretic mites away from the host. Many phorids occurred near the corner-posts supporting the trays where the flies appeared to be hibernating (BINNS *et al.* 1979). Here the compost was not wetted, so that it had not been colonised by mushroom mycelium and some

dry "casing" peat had come down from the trays above. About 150 ml of this dry debris was collected from each box and either (1) stored at 5°C (2) extracted by Tullgren funnel or (3) enclosed for the removal of phorids when the large numbers of mite bearing flies present in debris samples provided the material for the tests described.

An attempt was made to rear these mites using a moist 9 : 1 mixture of plaster of Paris and charcoal substrate in screw-top containers of various sizes. Food was provided in the form of unsterilised brewer's yeast, heaped in c 5 mg amounts, moistened and added, periodically, so as to maintain permanent cultures. None of the experiments required special equipment.

Through the cooperation of Dr. D. A. GRIFFITHS, scanning electron microscope photographs of mites in culture were made at the Pest Infestation Laboratory, Slough. Details of the techniques will be published in a further paper on the physogastric female.

RESULTS

Attachment

NORTON & IDE (1974) found that only the female mite attached to the host (cf. KARAFIAT, 1959). Usually a single mite attached medially to the second abdominal sclerite of the host, just anterior to a patch of setae. Where multiple attachment took place it often appeared that two additional females overlaid the original mite in an anterior position whereas other additions were made underneath the mites in front. Thus the mites clustered round the anterior abdomen, overlaying each other as do roof-tiles or shingles (Plate I). Where large numbers attached they spread more laterally and closer to the tergum.

Phoretic females showed great diversity in their degree of sclerotisation varying from dark brown to virtually transparent. Loads of phoretic scutacarids were also the focus of attachment by anoetid hypopi *Histiostoma* sp. (Acarina : Anoetidae), with as many as 26 per fly, which also stretched across to the hind femora (cf. CROSS & BOHART, 1969) in clustered incrustations which made detachments from large scutacarid loads more frequent. Flies confined over wet tissues, on which mushroom grain-spawn was allowed to develop, still carried scutacarids after 5 days enclosure. These were retained much more strongly than the anoetid hypopi which outnumbered the scutacarids by c. 50 : 1 in the washings of the containers.

The percentage of flies carrying mites (Table 1) in samples, excluding those from debris, varied widely from 4 to 78 % with a mean of 31 %. By comparison, between 58 % and 100 % (mean 87.6 %) of flies apparently hibernating in dry debris carried mite-loads. Compared with samples of flies taken simultaneously at Glasshouse Crops Research Institute, those from the bed debris were also very heavily parasitised (95 %) by the nematode *Howardula husseyi* (Nematoda : Allantonemidae). It is evident from this small sample of records that the proportion of infested phorids from different sources was widely divergent. Sex-ratio of hosts was female-biassed except in flies from debris samples in which the number of males and females was very similar (BINNS *et al.* 1978). It therefore seemed possible to distinguish subpopulations of attached mites around the farm.

The mean number of mites carried by flies from debris was 2.64 and the mean/variance ratio for all debris samples was 1.12, indicating a near random distribution. The mean number of attached mites taken elsewhere was 0.96 and the variance/mean ratio (in each of these cases, for twelve populations) was 2.42. Mites were, therefore, more aggregated, though fewer, on flies taken away from debris. These differences were significant (number, $t = 3.35$ $P < 0.003$; ratio, $t = 5.76$ $P < 0.001$).

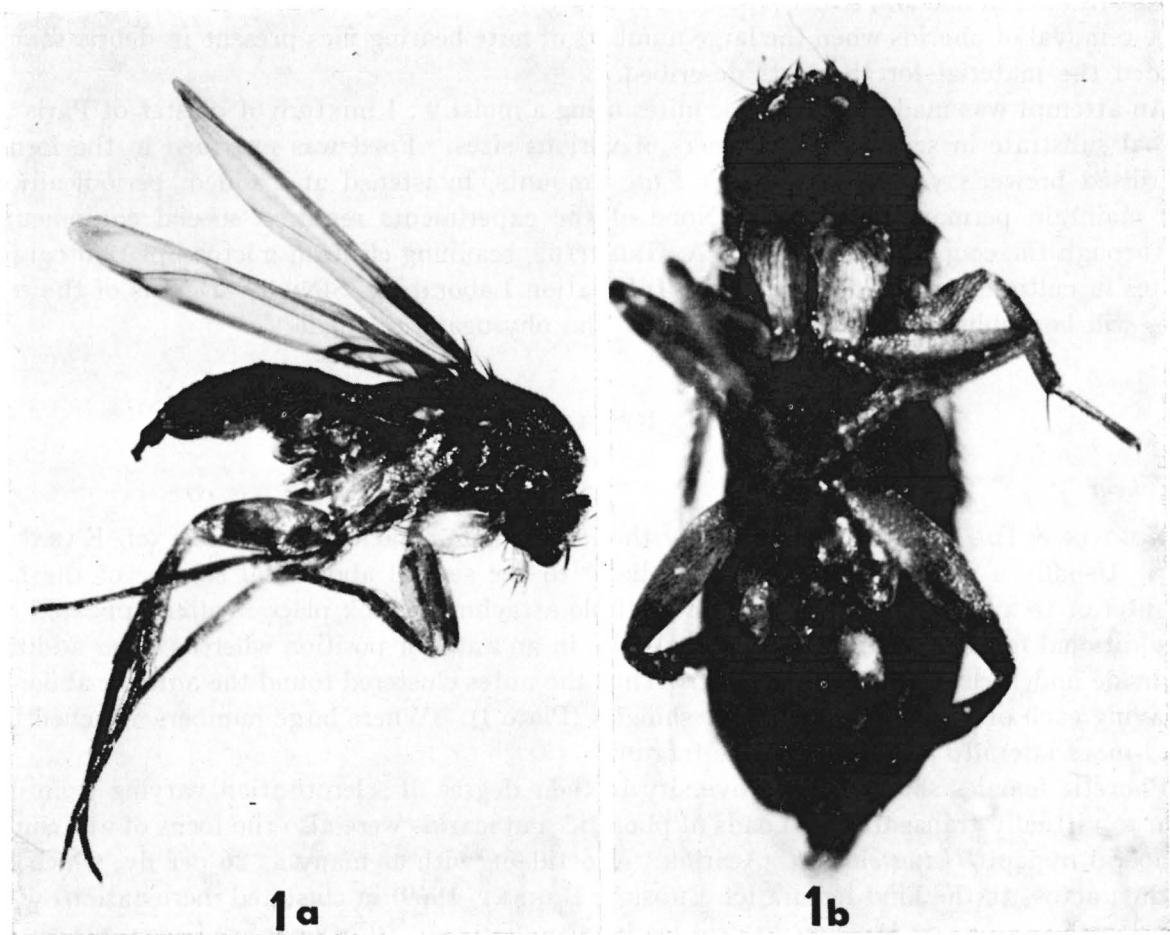


PLATE 1. — Phoretomorph females of *S. baculitarsus* clustered beneath anterior abdomen of phorid *M. halterata*.

When separate male and female counts were made of the frequency of attachment, a total of 12 distributions was available from the debris samples. When tested for goodness of fit against a Poisson distribution using a X^2 test these gave values between $P = 0.0012$ and $P = 0.997$ (mean 0.450) and showed a good fit to a Poisson distribution in 10 out of 12 cases. Very small X^2 probabilities were obtained from insects sampled away from the beds indicating a poor fit to a Poisson distribution as above.

The distribution of all mites both from debris and elsewhere was analysed (Table 2). The mites collected from flies hidden in debris were then shown to fit a negative binomial distribution (though only just) rather than the Poisson as above (Fig. I right). Flies found elsewhere were well described by the negative binomial distribution (Fig. I left).

A *t*-test of the differences between the proportion of each sex infested showed no significant differences ($P < 0.05$), either for those flies taken from debris (52 % female) or from elsewhere (54 % female) and it appeared that the sexes were equally infested as was found by CROSS & BOHART (1969).

Mites did not detach from infested hosts enclosed in tubes. Natural detachment was not observed but all attached mites left phorids decapitated while anaesthetised with carbon dioxide

unlike those examined by KARAFIAT (1959) and GREENBERG (1961). Detached mites readily reattached (within 24 h) to freshly introduced phorids and also to the sciarid *Lycoriella auripila* (Diptera : Sciaridae) from which they have not previously been recorded (cf. *Acarophonax triboli* (WADI & KISHORE, 1973)). Here, the attachment pattern was unchanged and proved the ability of the mite to "ambush" active, adult hosts (see below) rather than attach to teneral females or pupae (eg in *Blattisocius tarsalis* (TREAT, 1976) and in *Digamasellus fallax* (BINNS, 1973).

Table 1. Mite burdens on phorids taken from different sources around a mushroom farm

Source		Phorids with attached mites			
		Male flies		Female flies	
		Total sampled	% with mites	Total sampled	% with mites
Mushroom house	Position				
16	Under door	132	6	193	8.4
16	On door	179	23	292	26
22	On walls	47	66	64	78
22	Box sides	105	74	197	71
22	Debris 1	53 ⁺	100	58 ⁺	100
22	" 2	31 ⁺	58	32 ⁺	65
All	Debris	200 ⁺	86	201 ⁺	89
All	Other	1112	24.6	1674	26.7

⁺ Sex-ratio of flies from debris near unity.

Extractions

In one mushroom cropping-house in which the proportion of infested flies from debris samples was high, female scutacarids were recovered by Tullgren extraction from the casing, but not the compost layer.

Scutacarid mites were extracted from dry debris (first freed of flies) by Tullgren funnel together with small numbers of *Tyroglyphus putrescentiae* and *Parasitus fimetorum*. Large numbers of adult anoetid mites but few scutacarids were extracted from bed debris, first freed of phorids, using a modified Seinhorst apparatus. Samples of casing from the adjacent bed were free from these mites and the association of the anoetid hypopi and the scutacarid appeared to be limited to debris material. Due to early difficulties attributed to hot weather this house yielded c. 75 % of the normal crop of mushrooms. The casing was soil-like with a few rhizomorph strands. The compost smelled sharply sweet, was tan-coloured and virtually free from

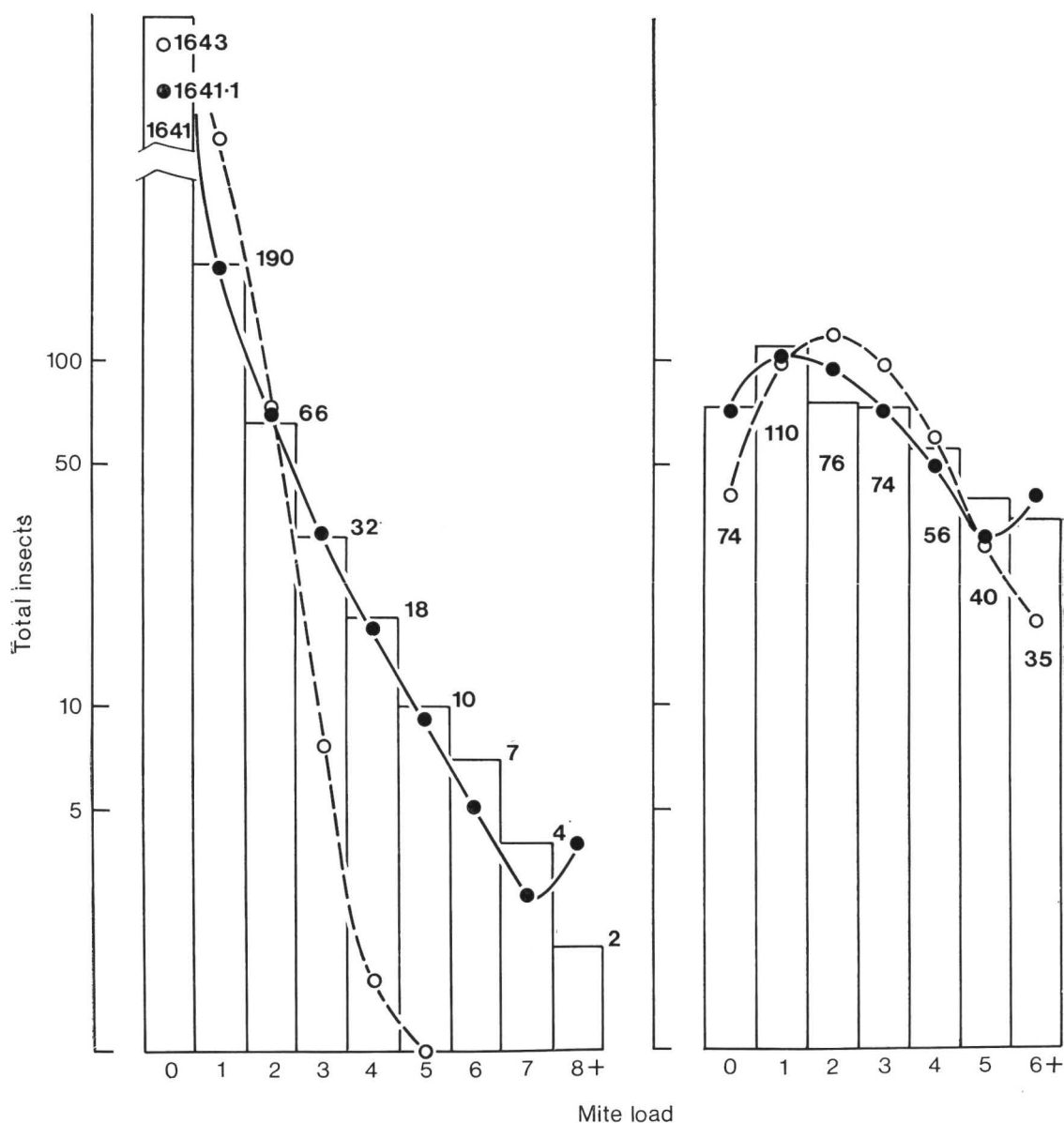


FIG. 1. — Frequency of attachment of phoretomorph females of *S. baculitarsus* in fly samples taken from bed debris (Right) and from sites other than bed debris (Left; see text) plotted against Poisson (open circles) and negative binomial (closed circles) distributions.

Table 2 - χ^2 probabilities with which observed data for mite burdens fitted two theoretical distributions.

	Fig.1 - flies from debris		Fig.2 - flies from elsewhere	
	Fitted χ^2	χ^2 for $P < 0.05$	Fitted χ^2	χ^2 for $P < 0.05$
Poisson	67.8	< 11.07 (5)	675	< 14.07 (7)
-ve binomial	9.12*	< 9.49 (4)	2.93*	< 12.59 (6)

Figures in parenthesis = degree of freedom; (*) asterisk = goodness of fit acceptable.

fungal mycelium except for some rhizomorphs. The number of nematodes at the end of the crop was 50-100 times greater than in the youngest crops and *Pygmephorus mites* (Acarina : Pyemotidae), indicative of weed moulds (HUSSEY, 1964), were also present.

When compost from this house was admixed with fresh compost and incubated the mixture was found to be contaminated by *Trichothecium roseum* (Gandy, D.G. ; G.C.R.I. personal communication), whereas the fresh compost was not. However, scutacarids were not recovered from compost which mite-bearing flies were exposed either when the compost was free from any known pest or disease and infested while mushroom mycelium was still running, or compost to which *Trichothecium roseum* inoculum had been added.

Host-finding

Perching stance Host-finding appeared to be a non-specific response which rapidly brought the phoretomorph female into exposed positions in the "perching" stance (Plate 2). In laboratory cultures females usually perched vertically on or near edges or corners. Alternatively, they would stand parallel with and across a vertical face with the venter facing outwards or jutting out horizontally from the vertical with the dorsum facing downwards (Fig. 2).

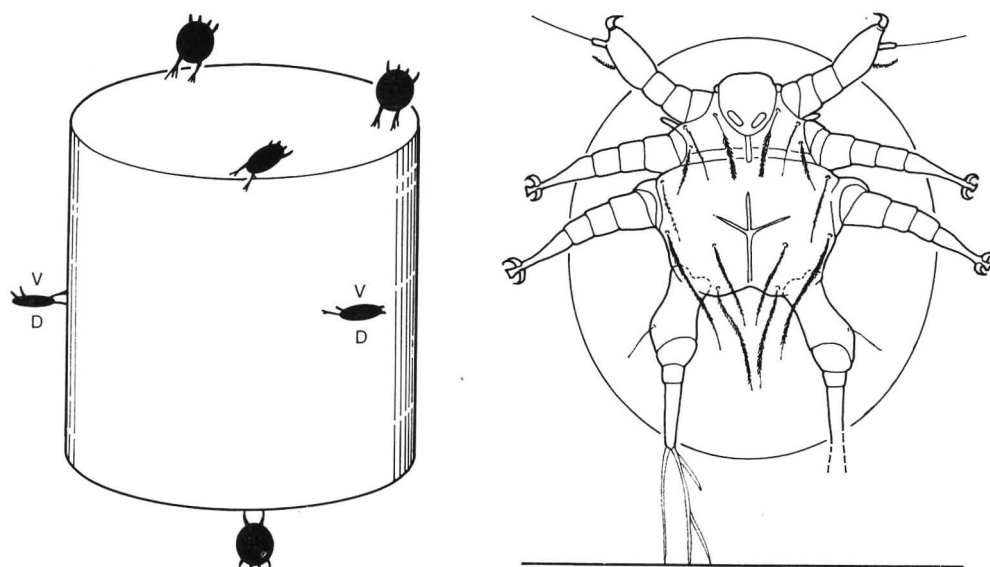


FIG. 2. — Range of perching attitudes in phoretomorph females of *S. baculitarsus* (D = dorsal, V = ventral surface).

FIG. 3. — Diagrammatic view of perching phoretomorph female of *S. baculitarsus* as seen under 80 × magnification.

On arrival at the perch the anterior rim of the body is raised by the bracing of leg I while the straightened leg IV is brought round and forward, below the raised venter, so that the mite leans over against the strain on this fully extended leg (Fig. 3), while the body is braced by the hindmost dorsal setae. This appeared to be a specialised function of leg IV which was trailed during locomotion and seemed to function only on cornering (cf. clasping leg IV of male which is specialised for carrying the chrysalis).

In some cases, adoption of the upright stance was preceded by movements in which the hindmost dorsal setae were repositioned on the substrate. Final assumption of the perching

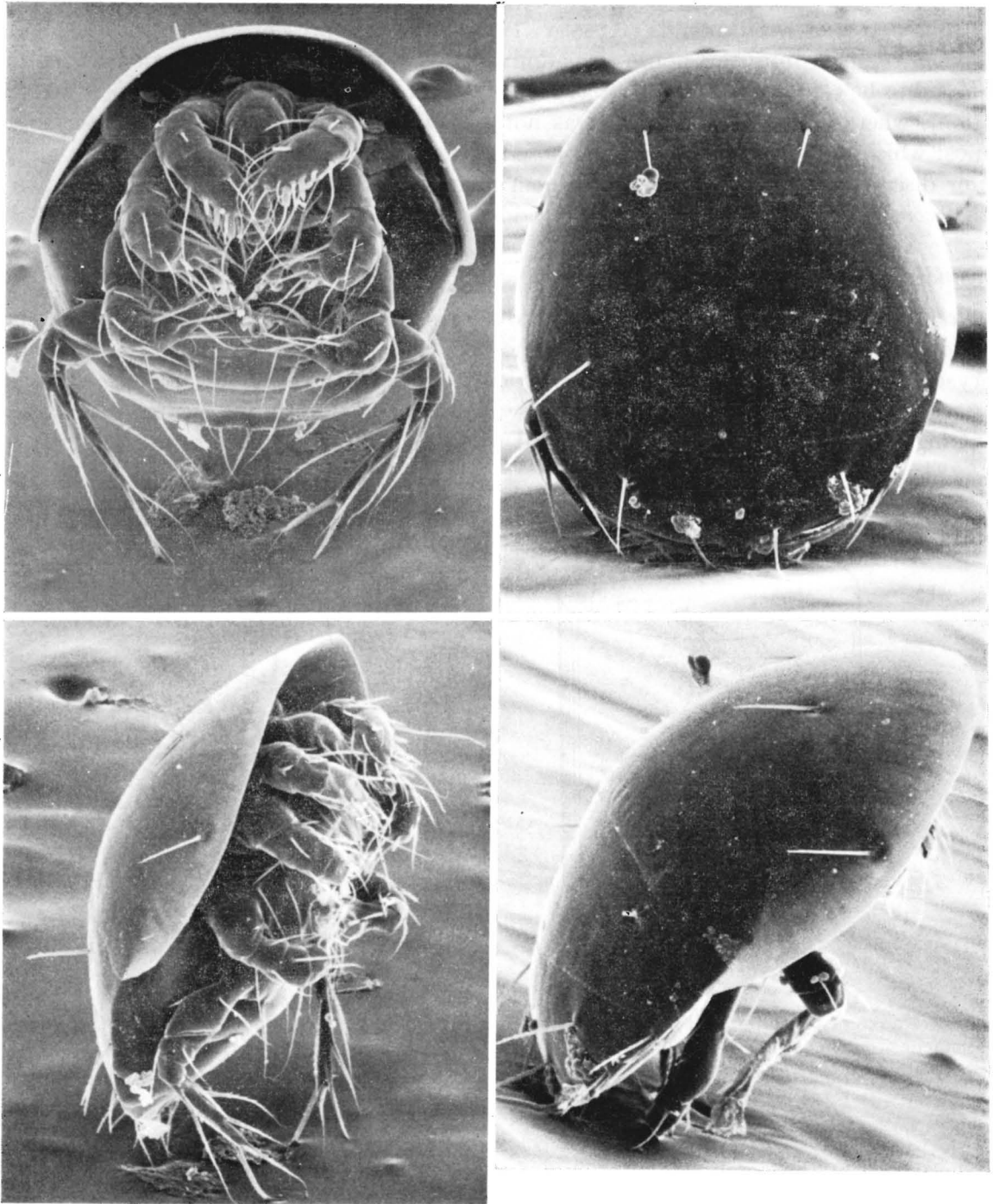


PLATE 2. — Views of perching-stance of phoretomorph females of *S. baculitarsus* (killed specimen under scanning electron-microscope).

stance was often preceded by some tight turning at the edge or up and down movements just below the edge (cf. movements of *Ixodes* LEES, 1948) where the mite finally perched. The slightest irregularity provided a perch eg. the back of larvae, the body of a host-fly or at the edges of a groove cut in the plaster substrate by a needle. Thus, many were found on small pieces of plaster placed in their pots, either on the top-most surface or along their edges. Similarly, in pots the greatest number were always found close to the gap around the periphery of the plaster. Thus, in one pot containing over 100 females, 98 were located round the periphery and only six on the central plaster. Mites either stood round the periphery, perching vertically, or just over the edge, perching horizontally. Such a distribution indicates an interruption of radial dispersive movements at an edge. In some cases the perch appeared to be an orientation to a common stimulus as in one pot where 50 females formed a line around the periphery and almost all appeared to face, tangentially, round the pot in the same direction.

Mites away from the periphery were most often mobile e.g. on a dry substrate or apparently feeding on moist brewer's yeast or showing signs of physogastry (see below) and, therefore, not perching. Fresh food was colonised by the motile larvae after approx. 3 days.

The anterior legs were held out in the perched position, with or without "Questing" movements (cf. those of *Ixodes* (LEES, 1948)). Attachment behaviour was immediately elicited by touching (eg) a fungal hypha on the outstretched legs. The mite was then "caught" on the thread with a speed which defied observation (cf. tactile response of hypopus of *Carpoglyphus*, OBOUSSIER, 1939).

The adoption of a vertical perching posture raises the question of the supporting mechanism. In no case could the anatomical mechanism of perching be discovered by up to 80 x magnification although there appeared to be four setae in contact with the substrate (Fig. 4). Most perching females were found on areas of plaster virtually free from fungus. Collection of females with a fine suction aspirator showed that they were more easily removed from bare plaster than from fungal material. Further, collecting one individual, using a minimum of suction, appeared to disturb the foothold of adjacent females apparently attached to the same or connected hyphae. Females secured to hyphae, in this way, could be pulled 45° from the vertical before they were dislodged showing how powerful was the grip on the substrate.

Response to light

The behaviour of phoretomorph females is characterised by weak responses to light and gravity.

Perched females were unaffected by slow or rapid alternation of light from two opposed microscope lamps though electronic flash photography caused jumping. This was also seen under the microscope though the mechanism was not clear and there appeared to be little control over direction or landing position. Females were confined in darkness in glass vials for 24 h and then tapped to the bottom of the tube which was then placed, horizontally, in the light beam so that they could either walk towards or away from the light. The mites walked from the base towards the lamp but, of a large number, none moved more than 1 cm without major divergences up the side of the tube or away from the light. In tubes facing away from the light many of the movements observed were photonegative and phototropotactic movements appeared weak.

Response to gravity

In two tests, ten (or four) glass vials (15 × 50 mm) with polythene stoppers were each loaded with 20 (or 15) females and left for 48 h (or 18) in the dark, fixed in a horizontal position. Only

10 % of the mites adopted positions in the upper half of the tube. Sixty-eight hours after encapsulation most mites occupied the lower half of the tube in nine cases out of ten, one tube having equal numbers. Rotation of the tubes showed that the mites could perch in the inverted position.

TABLE 3. Reactions of phoretomorph females of *S. baculitarsus* to gravity.

Observation	Position to gravity	Quadrants				Previously
		A	A ¹	B	B ¹	
1	A upper	23	26	16	15	24 h dark
	B lower					
2	B upper	21	26	18	13	3 h light
	A lower					
3	A upper	19	26	21	8	4 h light
	B lower					

Four 2 oz polythene pots, containing damp plaster on which four quadrants had been marked, were loaded with a total of *c.* 90 females. The pots were stood on their sides so that the plaster surface was vertical. The number of mites in each quadrant was counted after 24 h darkness. The pots were then rotated through 180°, to bring the lowermost quadrants to the top, after further periods of 3 and 4 hours during which the vertical lids of the pots were brightly lit by a 60 W lamp.

The numbers of mites on adjacent quadrants, labelled AA¹ and BB¹, after each period (Table 2) clearly show the relatively constant number in each quadrant irrespective of whether they represented the upper or lower-most portion of the surface. There was clearly no movement upwards, across the surface between observations and the mapping technique used showed the persistence of some groups of mites throughout.

Humidity ZAKHAVATKIN (1959) considered that one of the most important environmental changes necessitating movement related to humidity. Some evidence suggested that the perching attitude was less readily adopted on air-dry plaster surfaces on which, instead, females were seen closely adpressed to the substrate. In some cases mites were more active though perching was seen in such a container 10 h after loading with mites. A small amount of "Seelastrip" hygroscopic mastic attracted all the females in an unmoistened plaster pot.

Feeding Phorids were easily collected by inverting a funnel over the debris container. Samples of debris were however retained at 5°C to determine longevity under these conditions. The last flies bearing mites were collected 1 month after the material was obtained.

Females seemed well equipped to survive without feeding and therefore constituted a waiting stage as discussed by LINDQUIST (1976). Two groups of sixty-five mites collected in a pill box over moist filter paper were still in the perching position 1 wk after detachment. Under moist conditions, but apparently unsuitable for development, females lived for at least 3 wk. Similarly the phoretic stages of all four species discussed by CROSS & BOHART (1969) survived for at least 2 months without food.



PLATE 3. — Well-established colony of larval and adult physogastric females of *S. baculitarsus* on brewer's yeast.

Laboratory rearing

Scutacarids were successfully reared (cf. KARAFIAT, 1959) from phoretic females on charcoal/plaster of Paris plates to which unsterilised brewer's yeast was added in small amounts. This became contaminated with the fungus (*Mucor* sp.), though not severely where the number of scutacarids was high (Plate 3). The presence of the fungus did not appear to impede development and the mites' locomotory activities seemed well adapted to living among hyphae.

Attempts to set up cultures from phoretic females were not invariably successful but occasionally, large, immobile, physogastric females (Plates 4) of an orange colour with a dorsal white stripe, developed (as in *Acarophenax*; NEWSTEAD & DUVAL, 1918). Such forms were occasionally found, in spring, on grass (KARAFIAT, 1959). The physogastric forms varied greatly in size and tended to stay at the periphery of the fungus colony where they produced clear, spherical eggs in masses (Plate 5) consisting of 20-70 eggs built into a cradle of hyphae, often well above the plaster substrate. Egg masses were often produced *en masse* but could be slowly accumulated. The female was able to carry the egg on leg IV.

The first eggs were seen 10 days after enclosing phoretomorph females. The hatching of eggs was not always successful. Culturing from egg to egg required c. 24 days and early cultures produced only physogastric females.

The difficulty of handling all except the active phoretomorph females, the male and the eggs due to their immobility and the tendency of the other stages to adhere to whatever surface they touched, limited rearing methods to continuous mass culturing; individual cultures being kept for up to 3 months. This was done by sub-culturing of egg masses. At this time a small

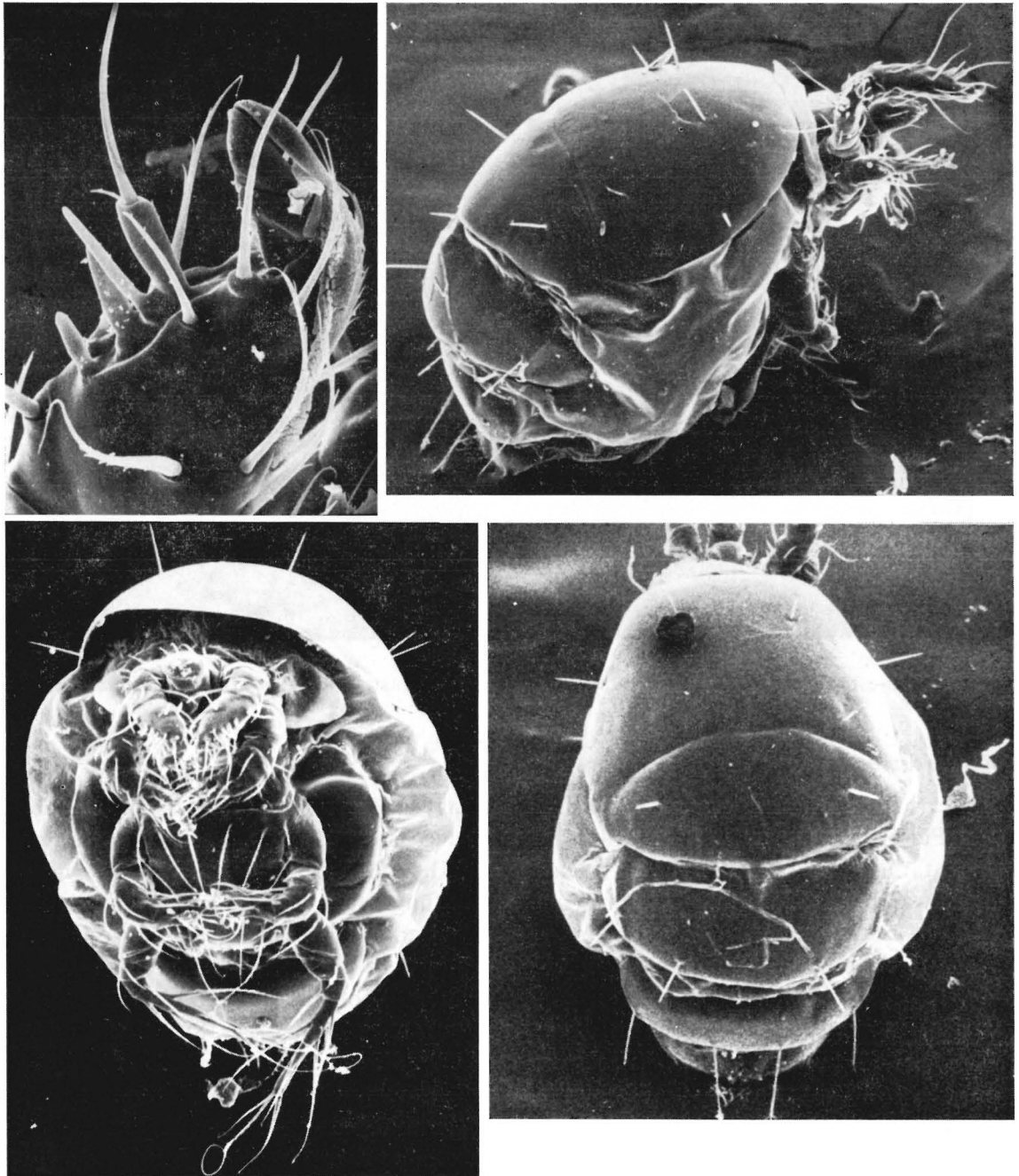


PLATE 4. — Views of female of *S. baculitarsus* in early stages of physogastry under scanning electron microscope (Upper-left : close-up of tibia of Leg I showing sensory adaptation and appposable claw).

but apparently mature, male was often discovered before the remainder of the eggs had hatched.

Details of the life cycle were not sought but this appeared to coincide with that described by SUSKI (1973) for *Siteroptes cerealium* (Kirchner) of egg, larva, chrysalis, adult.

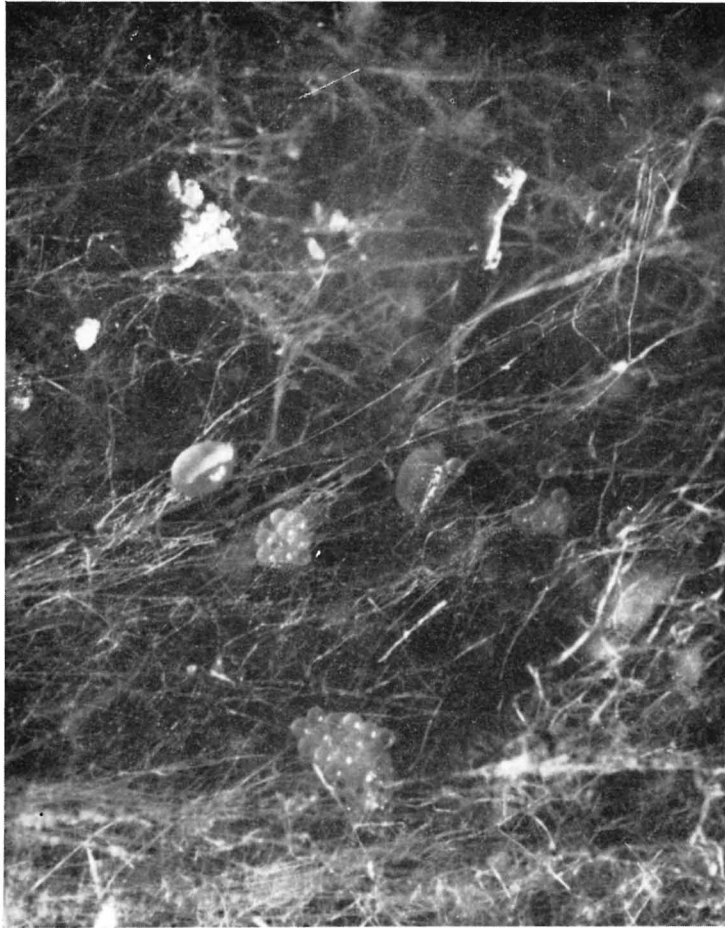


PLATE 5. — Egg-masses and physogastric female of *S. baculitarsus* in fungal web.

Towards the completion of their development the quiescent larve or chrysalis containing the phoretomorph female was carried in the clawed claspers (Leg IV) of the male (cf. ELBADRY *et al.*, 1976) and spaced out on parts of the plaster surface away from the feeding colony and uncolonised by fungus. Although the activities of the males as they clambered over the larval colonies appeared rather haphazard, it was assumed that these larvae, which contained the pharate female adult, would eventually produce phoretomorph females as these were frequently found in culture jars away from the feeding colonies.

Association of the males with the chrysalis was thought to be related to mating also since males (of which there were many) appeared to mate with the quiescent stage, often doing so from a cavity beneath the larva.

What factors governed the production of the physogastric forms from phoretomorph females and in established colonies was not clear.

No development occurred on plates of *Tricothecium roseum* on agar and the females tended to be smothered in spores. The adherence of these to the mite caused tracks to form on the agar uncolonised by fungus and clearly showed the alternate beating of the sensory forelegs, one of which was always ahead of the other.

DISCUSSION

NORTON & IDE (1974), describing the subspecies *agaricus*, refer to the examination of only eight phoretic mites. The discovery of large numbers of *S. baculitarsus* gave sufficient material to make biological observations both on host-finding and on the behaviour of this mite whilst in culture.

The geometry and statistics of attachment in a phoretic scutacarid were extensively studied by CROSS & BOHART (1969) and concerned the association between *Imparipes americanus* and the alkali bee *Nomia melanderi*. They also found a clustered, contagious distribution which differed little between the sexes and which was said to be over-dispersed (see SOUTHWOOD, 1966). However, this and the present example, where negative binomial distributions were found, confirm that this is the characteristic distribution of phoretic mites (BINNS, 1975) whereas, in the case of non-dispersing flies, from debris where the host-mite "transect" coincides (MITCHELL, 1969), the fit of the attached mites as measured for the individual populations by the mean/variance ratio indicated a Poisson distribution where no dispersal was taking place (cf. BINNS, 1975).

The existence of a phoretic relationship depends on some congruency in the habitat of the host and of the phoretic mite which may at the time require discovery. Thus the attachment of *Digamasellus fallax* (Leitner) to sciarid fungus gnats (BINNS, 1973) reveals the increase in the numbers of nematodes, on which the mite feeds, shortly after oviposition by the fly. In phorids the numbers of such associations is limited (see HUSSEY, 1959) since the insects only known resource is the growing mushroom mycelium (HUSSEY & WYATT, 1962). Ideally this is grown in pure culture but under some circumstances a "weed-mould" e.g. *Tricothecium roseum* growing relatively close to the mushroom mycelium, may bring a perching scutacarid and a foraging phorid into contact. Since there is no necessary association between phorids and *Tricothecium roseum*, the phoretic association must be considered facultative with respect of the host species, which is assured only by ecological circumstances. While this association with phorids might easily be overlooked, its apparent rarity (and of other associations with phorids) (HUSSEY, 1959) may result from the rigorousness of the requirements of the fly. In addition to raising the question, what microhabitat the mites are being transported to, their attachment to both male and female flies indicates that, with respect to mite-attachment, the spheres of activity of male and female flies have more in common than is sometimes apparent (HUSSEY, READ & HESLING, 1969). This seemed particularly true of hibernating flies in which the sex-ratio was approximately equal (BINNS, *et al.*, 1979).

Phoretic attachment requires gripping of the host either by sucker plates, glue strands, the legs or the chelicerae. Since the modification of the stylet-like chelicerae of scutacarids (ATHIAS, 1973) prevents their use in attachment, they attach by their claws. The method of attachment to the integument in *S. baculitarsus*, does not confirm the suggestion of CROSS & BOHART (1969) that the claws of leg I are adapted for grasping the setal bases of the thoracic pile as they describe in *I. americanus*. The proportion of female scutacarids in which leg I is provided with a claw is higher in phoretic species (DELFINADO & BAKER, 1976) than in species (e.g. of *Variatipes*) collected in moss (KARAFIAT, 1959) and other apparently free-living species (DELFINADO, BAKER &

ABBATIELLO, 1976). A well developed claw is found in some scutacarids and pyemotids. It appears that in scutacarids, e.g. *S. baculitarsus*, this is related to the method of host-capture by "ambush" or lying in wait in the "perching" position. In Mesostigmatid mites e.g. *Parasitus* and *Macrocheles*, leg I has a sensory function enabling stalking of the host and this, as in *S. baculitarsus* (see NORTON & IDE, 1974 and plate 4-upper left), in general, characterises a phoretic instar rather than the presence of a claw (EVANS, G. O., *In litt.*).

The adoption of, usually elevated, perching positions is found in the Trombidiid *Leptotrombidium scutellaris* (SASA, 1963) and in the tick *Ixodes ricinus* (LEES, 1948). A possible mechanism of leg IV during "perching" is suggested by the figure for *Pygmodyspus* of MAHUNKA (1965) in which the tibiotarsus is provided with a central hooked process which might exert a straining force braced by the surrounding pliant, barbed, setae on the principle of a sheathed 'Bowden' wire. In this way, provided the force exerted by the claw is greater than the gravitational pull on the body, "perching" even from an overhead substrate can be explained. However the progressive reduction of the setae to a single process, as in *Peridispus foliiger* (ATHIAS, 1972) would render it impossible. Similarly the reduction of the number of setae and the loss of the central ambulacral process of the tibiotarsus preclude such a mechanism in *S. baculitarsus*. Instead the tibiotarsus which is elongated (as in *S. longitarsus* (see fig. 3 and RACK, 1964)), which is phoretic on *Heterocerus* (KARAFIAT, 1959)), carries only four proximal and three terminal setae. The longest of the latter carries a series of barbs (figured by NORTON & IDE, 1974) which might serve to grip the substrate. Long terminal setae on legs IV in many cases characterises a phoretic instar (LINDQUIST, 1975). Beyond allowance by the elongated tibiotarsus of the leaning-back, "perched" position, the perching mechanism is still unclear. However, Leg IV is slightly shorter in the non-phoretic morph (Norton, R. A., State University of New York, personal communication). Mainly phoretic material was examined and there was no evidence of polymorphism (cf. SMILEY & MOSER, 1976).

The limited repertoire of behaviour in *S. baculitarsus* suggests that the "ambush" position is adopted as rapidly as possible, whatever the conditions and that active searching period of phoresy, apart from perching, is short. Thus SATCHELL & NELSON (1962) noted that these mites appeared ill-adapted for movement, hence their extraction from soils is facilitated by floating rather than Tullgren extraction. On the other hand, their flattened aspect, reminiscent of acarid hypopi, fits them for phoretic attachment and minimises both the risk of being brushed off the host (LINDQUIST, 1975) and exposure to dry atmospheres.

Among the tarsonemids, a series exists extending from the precociously appearing male scutacarid through the early-appearing male Pyemotid ectoparasitic on the female (KRACZAL, 1959), to the male of *Acarophenax* which is lodged inside the female (NEWSTEAD & DUVAL, 1918). The males of *Pediculopsis graminum* (Reut.) (= *Siteroptes cerealum* (Kirchner)) appear to represent an intermediate stage. Copulation usually occurs within the maternal body although males (and females) are often found wandering over the abdomen of the pregnant physogastric female (COOPER, 1937). In *Acarophenax* the male never leaves the body of the mother. In *S. agypticus* the male emerges 1.4 days before the female who's generation period occupies 7.5 ± 1.2 days (ELBADRY *et al.*, 1976).

ACKNOWLEDGEMENT

I thank Prof. G. Owen EVANS, University of Dublin, for determining *Scutacarus baculitarsus* and, together with Dr. N. W. HUSSEY, G.C.R.I., and Dr. D. A. GRIFFITHS, Pest Infestation Laboratory, for comments on the manuscript. Dr. GRIFFITHS also conducted scanning electron microscopy.

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Paru en Janvier 1980.
